AMAZONIANA XII (1/2): 53-63 Kiel, Dezember 2002

Influence of the flood pulse on leaf phenology and photosynthetic activity of trees in a flooded forest in Central Amazonia/Brazil*

by

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(Accepted for publication: July, 2002).

Abstract

This study was carried out over a four-year period in a blackwater flooded forest (igapó) on lower Tarumã-Mirim River, Central Amazonia, in order to verify the influence of the flood pulse on the phenology and photosynthesis of two tree species, *Eschweilera tenuifolia* (Lecythidaceae) and *Hevea spruceana* (Euphorbiaceae). Phenology and photosynthesis were monitored weekly. Photosynthetic activity was measured on sun leaves, through infra-red gas analysis (IRGA). Both species are semi-deciduous and their distribution occurred mostly on the lower levels of the floodplains that remained flooded for longer and eventually uninterrupted periods. Monthly maximum mean assimilation rates of CO_2 (A_{max}) are related to photosynthetic activity and leaf age, mature leaves of *H. spruceana* showed maximum A_{max} of 9.5 µmol m^{-2} s^{-1}, whereas for *E. tenuifolia* the value was 8.8 µmol m^{-2} s^{-1}. The seasonality of leaf fall seems to be a response to environmental change related to the period of high irradiance levels.

Keywords: **Leaf phenology, assimilation rates of CO_2, irradiance, *Eschweilera tenuifolia*, *Hevea spruceana*, igapó.**

Resumo

Este trabalho foi desenvolvido ao longo de um período de quatro anos, em uma floresta de inundação por água preta (igapó) no baixo rio Tarumã-Mirim, Amazônia Central, objetivando verificar a influência do pulso de inundação sobre a fenologia e fotossíntese de duas espécies de árvores, *Eschweilera tenuifolia* (Lecythidaceae) e *Hevea spruceana* (Euphorbiaceae). A fenologia e a fotossíntese foram monitoradas semanalmente. A atividade fotossintética foi medida em folhas totalmente expostas ao sol, por meio de um analisador de infra-vermelho (IRGA). Ambas as espécies são semi-decíduas e sua distribuição centraliza-se principalmente nos níveis mais baixos das planícies inundáveis que permanecem alagadas por períodos mais longos e, eventualmente, ininterruptos. As médias mensais máximas de taxas de assimilação de CO_2 (A_{max}) relacionaram-se à atividade fotossintética e à idade das folhas; folhas maduras de *H. spruceana* apresentaram o valor máximo de A_{max} de 9.5 µmol m^{-2} s^{-1}, enquanto que para *E. tenuifolia* esse valor foi 8.8 µmol m^{-2} s^{-1}. A sazonalidade na queda de folhas parece ser uma resposta a mudanças em fatores ambientais relacionadas ao período de maiores níveis de radiação solar.

*Dedicated to Prof. Dr. Harald Sioli on the occasion of his 90th anniversary.

ISSN 0065-6755/2002/053/ © MPI für Limnologie, AG Tropenökologie, Plön; INPA, Manaus

Introduction

In the seasonal dry tropics, the water-related factors may be a primary influence on phenological patterns, whereas in the humid tropics, the degree of irradiance may exert a strong influence on them (VAN SCHAIH 1986). Vegetative and reproductive developments in tropical forests are periodical even if seasonal variations in temperature, water availability and photoperiod are small (BORCHERT 1992). Within Amazonia, variability in the pattern of distribution of precipitation throughout the year is reflected by different periods of flowering and fruiting at a regional level (DUCKE & BLACK 1953). In the savannahs on the lower Amazon River, such as Alter-do-Chão (Santarém), the peak of leaf fall correlates with lower precipitation and higher temperature levels as well as the period of water shortage in the soil (MIRANDA 1991). On terra firme, at Reserva Florestal A. Ducke near Manaus, peaks of leaf fall and flowering correlate with the lowest precipitation levels (ALENCAR 1999; ARAUJO 1970).

In Amazonian floodplain forests the periodicity of the vegetative activity is seasonal and appears to be a result of environmental factors. Fall of old leaves, production of new leaves, flowering, and fruiting relate in several cases to the river level fluctuation (FERREIRA 1991) that in Central Amazonia shows an annual average of 10 m. On the other hand, leaf phenology may be a result of the presence of ethylene due to the anoxic conditions in soil and water as a result of the length of inundation (JOLY & CRAWFORD 1982; SCHLÜTER et al. 1993). The importance of knowing the phenology of arboreal species in the Amazonian floodplains and its relation with environmental factors, have increased the interest this subject in the last ten years (REVILLA 1981, 1991; KUBTIZKI & ZIBURSKI 1994; MAIA 1997; MAIA et al. 1998; MAIA & PIEDADE 2002; OLIVEIRA 1998; FERREIRA 1991, 1998; WITTMANN & PAROLIN 1999; PAROLIN 2000).

Although the photosynthetic capacity varies among arboreal species, some specific phenologic categories may show a typical range of defined values (LARCHER 2000). Leaf life span is one of the factors defining this range (MAIA 1997; MOONEY & GULMON 1982; PRADO 1994). Deciduous species usually show a higher photosynthetic capacity in comparison to the evergreens (SESTÁK et al. 1971). Nevertheless the relation between leaf phenology, photosynthetic activity and flood pulse is poorly understood (MAIA 1997; PAROLIN 1997; MAIA & PIEDADE 2002).

In order to fill this gap, the present work integrates results on leaf phenology and photosynthetic activity of two ecologically and economically important tree species from the blackwater floodplain forest (igapó), *Eschweilera tenuifolia* (Lecythidaceae) and *Hevea spruceana* (Euphorbiaceae), verifying the influence of environmental change related to period of high irradiance levels and flood pulse in those two parameters.

Material and methods

Study site, hydrology and species: The field work was carried out from January 1992 to December 1995 at a site in the lower Tarumã-Mirim River (3°02'S, 60°17'W) about 20 km upstream from Manaus. The study site of 500 x 50 m was located along the margin of a stream, 20 to 23 m above sea level.

The climate of the area is hot and humid with monthly minimum mean temperatures ranging from 22.9 to 23.8 °C, with a maximum from 30.2 to 33.3 °C, relative humidity of the air at 1 m varied from 75.6 to 86.7 %. Precipitation ranges from 1000 to 2500 mm (IRMLER 1975). Figure 1 shows the study area patterns of monthly sums of insolation hours and precipitation and monthly mean averages of the relative humidity as well as the Rio Negro water level at Manaus harbour. Even if the monthly frequency and intensity of precipitation are different 20 km away (RIBEIRO & ADIS 1984), the seasonal patterns of rainfall are similar in the vicinity of Manaus. The annual variation of the water level shows a mean range of around 10 m.

Study area vegetation is divided in two regions, the low and high igapó (ADIS 1984). The lower region is represented by several shrubs and species of lower height, among them *Myrciaria dubia* (Myrtaceae), *Symmeria paniculata* (Polygonaceae) and *Bactris maraja* (Arecaceae). This region may have individuals reaching up to 16 m in height, as *Hevea spruceana* (Euphorbiaceae). At the high igapó, where the canopy is more dense with emergent trees about 25 - 30 m tall, the species *Aldina latifolia var. latifolia* (Papilionoideae), *Swartzia polyphylla* (Papilionoideae) and *Eschweilera parviflora* (Lecythidaceae) predominate.

Species phenology: phenological observations were made for 4 years, from January 1992 to December 1995, on a weekly basis on 15 individuals of each species, randomly selected in the study area. In each individual, five branches on the mid and upper parts of the canopy were labelled and followed-up in order to record changes related to leaf age.

Leaf production and abscission were defined as: new leaves - up to two weeks after the appearance of the first foliar buds; mature leaves - from two weeks up to 8 months of development; old leaves - from 8 to 10 months after new leaves appearance and yellowish in colour. The percentage of leaves on the crown above the water level was calculated according to subjective observations.

Photosynthetic activity: measurements were made for 18 months from July 1993 to December 1994, carried out on a weekly basis on three individuals of each species. The assimilation rate of CO_2 (A) per unity of leaf area was measured through the infra red gas analyser (IRGA) technique, using an open gas exchange portable LCA 2 Infra Red Gas Analyser (ADC Ltd., Hoddesdon, UK). For each measurement in the field a leaf from the selected trees was placed in a leaf chamber with a 12 cm^2 area of exposition to the sun (PARKINSON Leaf Chamber). A controlled and measured air rate was supplied (ASU, ADC Ltd.) to a leaf cuvette (PLC, ADC Ltd.). the leaf was placed in a leaf chamber (PARKINSON Leaf Chamber). A controlled and measured air rate was supplied (ASU, ADC Ltd.) to a leaf cuvette (PLC, ADC Ltd.). Concentration changes of water vapour along the cuvette were measured with a capacitance humidity sensor (LDC, ADC, Ltd.). To determine the maximum CO_2 assimilation rates (A_{max}) performed by the species, five sun leaves of each species of the canopy top were measured weekly between 8:30 a.m. and 3:30 p.m.. Only fully expanded and intact leaves without holes or epiphytic infections were used. All measured leaves were permanently subjected to full light conditions. Changes of photon flux densities ranging from 0 to 2000 µmol m^{-2} s^{-1} were obtained using neutral density filters which were placed above the chamber window to vary the light level on the leaf surface. The measurements of each plant comprise the four critical phases along the hydrological cycle: terrestrial phase, rising water, peak of inundation, and receding water.

Results

The studied species can be considered as semi-deciduous trees since during the study period they kept a minimum of mature leaves (Fig. 2A, C) during the period of the year with less precipitation and humidity, and high irradiance levels (Fig. 2B).

Peak of leaf fall in *H. spruceana* was towards the end of April, when nearly 70 % of all the leaves were old, which correlates with the beginning of lowest precipitation and humidity and highest irradiation levels (Fig. 2A, B). The production peak of new leaves was between May and June, the period of high water levels (Fig. 2A).

Maximum leaf abscission for *E. tenuifolia* was between June and August, the period of lowest precipitation and humidity, and of highest irradiation levels in the region (Fig. 2B, C). In August, the remaining old leaves in the crown above the flood water was about 40 % of the total amount of leaves. Partial leaf fall and peak production correlate with the beginning of receding waters, between August and September (Fig. 2C).

For both species the peak of leaf production was simultaneous and the mean life span of the leaves ranged between 8 and 10 months. The maximum production of new

leaves (Fig. 3A, 4A) always preceded flowering and fruiting (MAIA 1997).

The leaf fall of *E. tenuifolia* and *H. spruceana*, appears to be more related to irradiance than to other climatic factors, the peak of *E. tenuifolia* leaf fall coincides with the high period of irradiance and *H. spruceana* show strong leaf fall in the beginning of the irradiance elevation (Fig. 2A, B, C).

Higher values of CO_2-assimilation rates in leaves of *H. spruceana* were found between July and March when the crown had 85 % to 100 % of mature leaves in relation to the total amount of leaves. From April to May, when precipitation levels diminished and the percentage of mature leaves declined due to the peak of senescence and new leaf production, the lowest CO_2-assimilation rates at leaf level were measured (Fig. 3A, B).

For *E. tenuifolia* the higher values of leaf CO_2-assimilation rates were obtained between September and May, when 75 % to 100 % of leaves on the crown were mature. The values of CO_2-assimilation declined between June and August when the peak of senescence occurred and new leaves were produced, period corresponding with the lowest precipitation (Fig. 4A, B).

Mean value of CO_2-assimilation of mature leaves of *E. tenuifolia* was 8.8 $\mu mol\ m^{-2}\ s^{-1}$ while it was 9.5 $\mu mol\ m^{-2}s^{-1}$ for *H. spruceana* (Fig. 3B, 4B).

Discussion

On the Amazonian terra firme forest, leaf fall is mainly correlated with the dry season (ALENCAR et al. 1979; KLINGE & RODRIGUES 1968), while in floodplain forests most species show leaf fall during the high water period. Among others, water level fluctuations appears to be an important trigger for the phenology of several species (SCHÖNGART et al. 2002).

The igapó forest seems to be mostly composed of evergreen species although a detailed analysis shows that evergreen and deciduous species do exist in both whitewater (várzea) and blackwater (igapó) habitats (WORBES 1997). In the igapó and várzea forests of Central Amazonia, correlation of abscission and leaf production in a given period of the year indicates that these forests show a seasonal pattern characteristic to woody semi-deciduous or deciduous species (MAIA & PIEDADE 2002). Both species studied can be considered as semi-deciduous trees since during the study period they kept a minimum of mature leaves.

The atypical high water levels observed in 1993 and 1994 resulted in a longer period of inundation for the species located on the lower levels in the flood plains, about 19.5 m (a.s.l.) remained the individuals with their roots and the lower portions of the trunks inundated for about 690 days (MAIA, 1997), suggesting the existence of a specific metabolism and a high degree of selection concerning species distribution in the colonizing of these environments (JUNK 1989; MAIA et al. 1998). However, a longer period of inundation appears to have no effect on the leaf chronology in both species (MAIA 1997; MAIA & PIEDADE 2002), indicating that other environmental factors could act as trigger for phenological events. On the other hand, inundation seems to prompt seasonal patterns in leaf change for some species. The tree *Vatairea guianensis* (Fabaceae), when cultivated on terra firme, remains evergreen while in the igapó forest the change of leaves is seasonal, showing that the flood may be a trigger for determining leaf chronology in this species. This strengthens the hypothesis that, for some species in floodplain forests, the flood pulse, rather than endogenous factors, may determine

phenology (MAIA 1997).

Nevertheless, studies have shown that a number of different reactions to the flood may be present for different species of plants, indicating different adaptation strategies for the change between the aquatic and terrestrial phases. It has been demonstrated that some of the phenological phases are linked to changes in ethylene concentrations that, being higher during the aquatic phase, promote premature abscission not only in leaves, but of flowers and fruits as well (JACKSON 1985; JACKSON & OSBORNE 1970). In the igapó a maximum of leafless species is observed during the late aquatic phase (WORBES 1997). Observations on the phenology of trees in the várzea indicate, that for some species the main period of abscission and new leaf production is not directly related to the flood pulse (WITTMANN & PAROLIN 1999). In some other cases, leaf-fall is correlated with maximum insolation and water level (ADIS 1984; VAN SCHAIH 1986), and its peak may be associated to the dry season (FRANKEN et al. 1979). The period of *E. tenuifolia* leaf fall and *H. spruceana*, appears to be more related to irradiance since the important environmental change occurred in this period was the irradiance elevation. When growing on terra firme, *H. spruceana* shows a similar phenological behaviour compared to the igapó forest, suggesting that water-related factors are not of primary influence on its phenological pattern. Interaction of a number of biotic and abiotic factors may play a role on the vegetation responses which depends on the species and time of colonisation of a specific habitat (PIEDADE et al. 2001).

Phenological studies in tropical rain forest trees have shown that any further conclusion should take the complexity of climatic, edaphic, genetic, botanical and ecological factors into account (ALENCAR 1999; MAIA 1997; MAIA et al. 1998; SCHÖNGART et al. 2002). Such factors plus the complementary study of floodplain trees planted on terra firme should be encouraged in order to elucidate the main trigger factors in determining the phenology of floodplain forest species (MAIA 1997; MAIA & PIEDADE 2001).

The photosynthetic capacity of deciduous trees ranges between 6.3 and 15.7 $\mu mol\ m^{-2}\ s^{-1}$ (SESTÁK et al. 1971). In nutrient-poor floodplains, this value is around 8.4 $\mu mol\ m^{-2}s^{-1}$ (SMALL 1972). The CO_2-assimilation between 8.8 and 9.5 $\mu mol\ m^{-2}s^{-1}$ for *E. tenuifolia* and *H. spruceana*, strengthen the classification of both species as semi-deciduous woody plants of the blackwater igapó (MAIA 1997).

Conclusions

The seasonality of leaf fall seems to be a response to environmental changes related to the period of high irradiance levels;

The seasonal change of leaves determines the periodical variations in leaf CO_2 assimilation rates throughout the year for *H. spruceana* and *E. tenuifolia*;

Monthly maximum mean assimilation rates of CO_2 (A_{max}) are related to photosynthetic activity and leaf age.

Acknowledgments

The authors would like to thank INPA and the SHIFT Program of the Brazilian-German Cooperation (CNPq/IBAMA/BMBF/DLR) for financial support, through the Project ENV 29, the INPA/Max-Planck Project and the PPG-7/PPP. We thank INPA for logistic support, and the skilful help in the field of the technicians of the CPBO/INPA Co-ordination, José Guedes, José Ramos and Cosme Damião.

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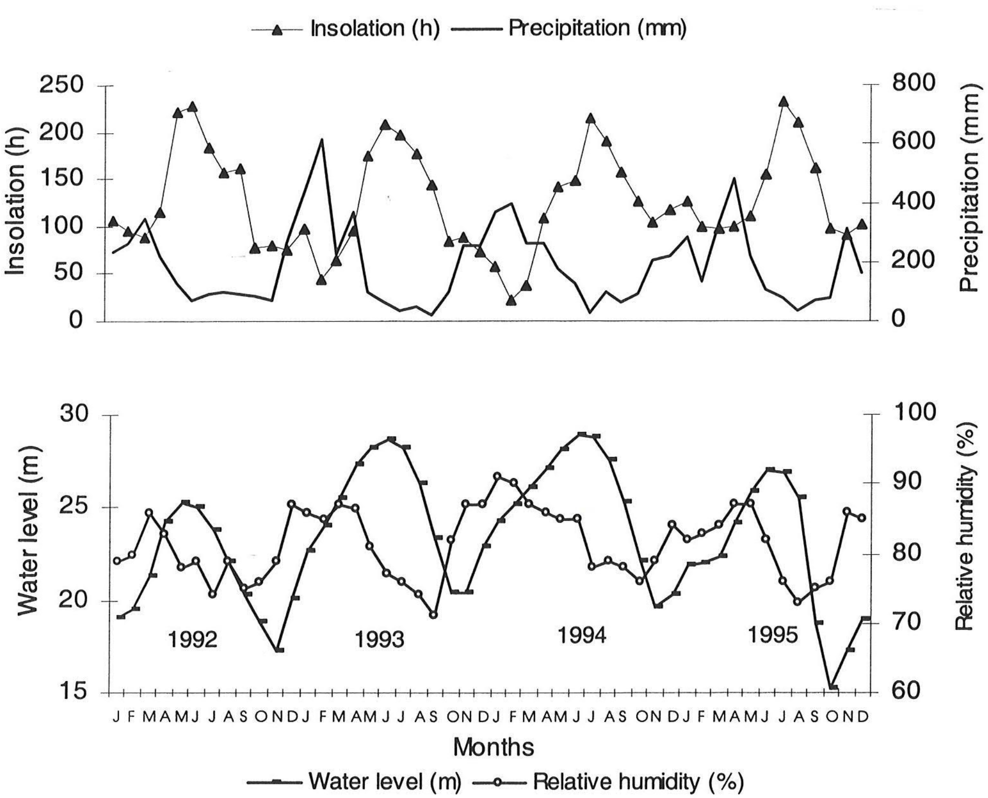

Fig. 1:
(**A**): Monthly sum of insolation (h) and precipitation (mm); (**B**): monthly average of relative humidity (%) and Rio Negro water level (m) at Manaus harbour. (Insolation, precipitation and relative humidity data provided by the Agriculture station Manaus-AM).

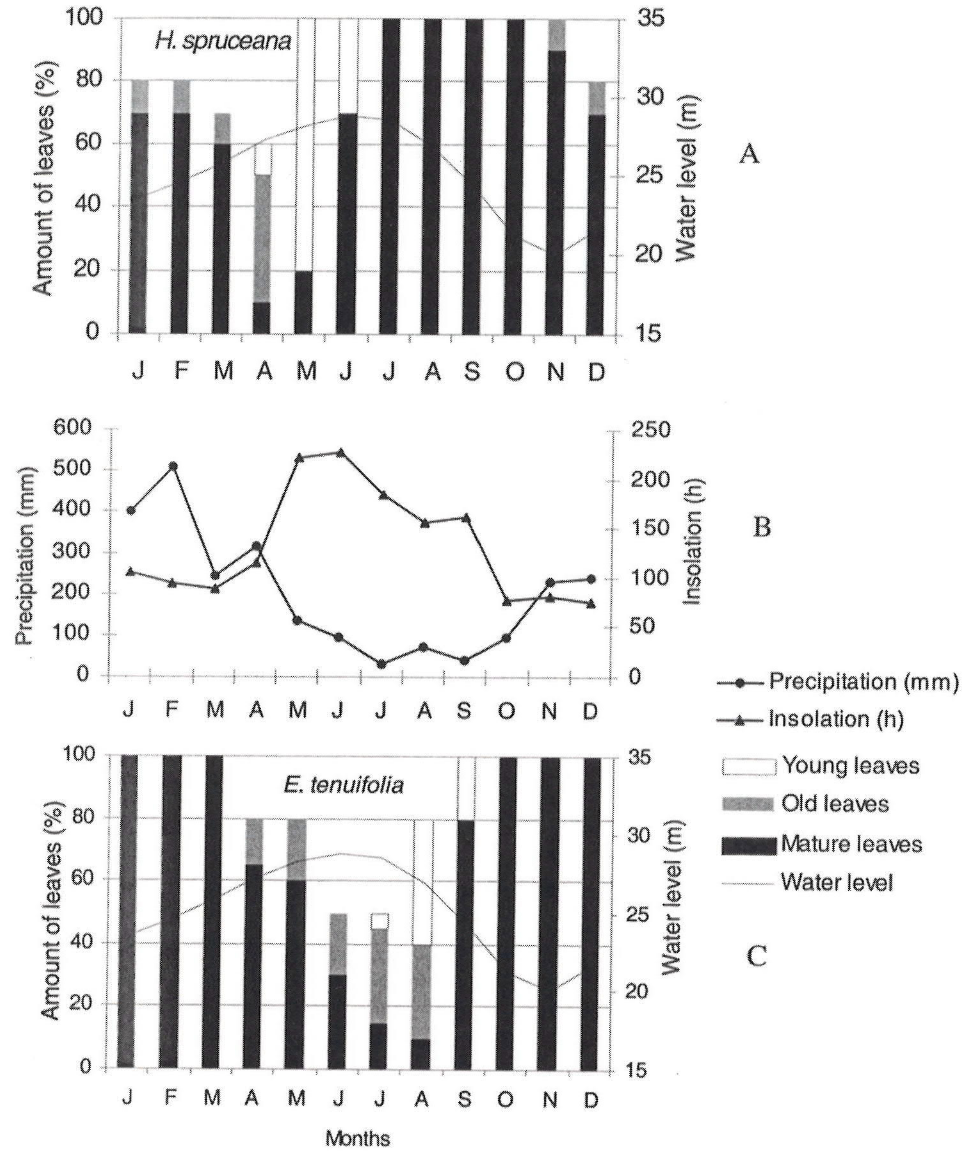

Fig. 2:
(**A**): Monthly amount of leaves (%) of *H. spruceana*; (**B**): monthly sum of insolation (h) and precipitation (mm) during the study period; (**C**): monthly amount of leaves (%) of *E. tenuifolia*.

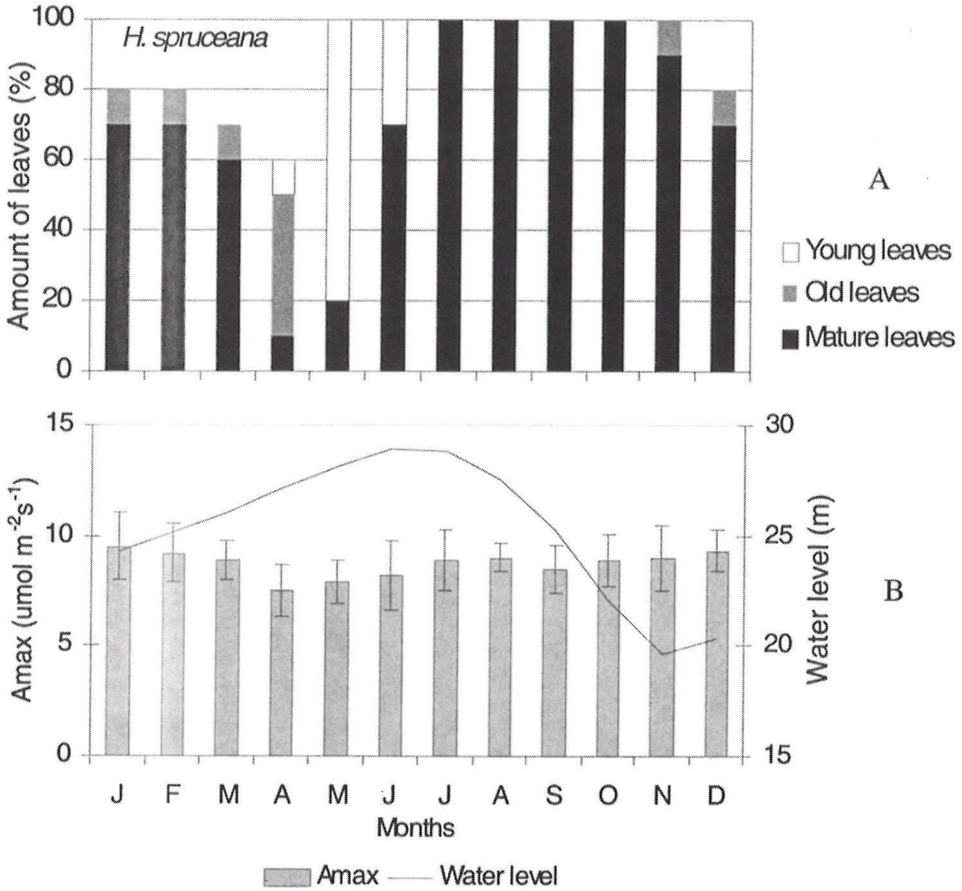

Fig. 3:
(**A**): Monthly amount of leaves (%) of H. spruceana; (**B**): monthly mean CO_2 assimilation rates (A_{max}).

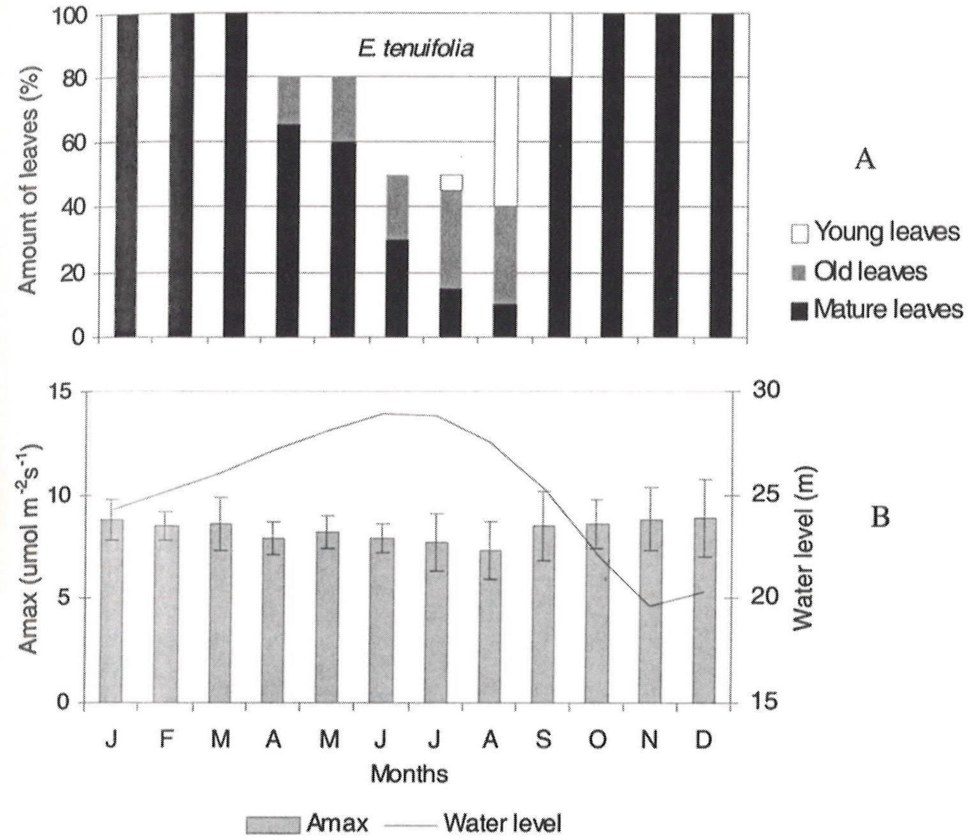

Fig. 4:
(**A**): Monthly amount of leaves (%) of E. tenuifolia; (**B**): monthly mean of CO_2 assimilation rates (A_{max}).